

Evolution of Intragonadal Development in the Diminutive Asterinid Sea Stars *Patiriella vivipara* and *P. parvivipara* with an Overview of Development in the Asterinidae

M. BYRNE AND A. CERRA

Department of Anatomy and Histology, F-13, University of Sydney, N.S.W. 2006, Australia

Abstract. The diminutive asterinid sea stars *Patiriella vivipara* and *P. parvivipara* incubate their embryos in the gonads to the advanced juvenile stage. Despite the small size of their eggs (135–150 μm diameter), development is lecithotrophic. Development proceeds through the wrinkled blastula, gastrula, and brachiolaria larval stages. The gastrulae and larvae are uniformly ciliated and swim, propelled by the cilia, in the gonadal fluid. The brachiolaria is pear-shaped and has a vestigial brachiolar attachment complex composed of three small brachia. At no stage in development are the embryos attached to the gonad. Metamorphosis occurs as the larvae swim in the gonadal lumen. Internal development involves formation of one large enterocoel at the anterior end of the archenteron and one small posterior enterocoel on the left side of the archenteron. The archenteron closes to form the rudiment for the adult gut. As a result of the small size of the egg and the nonfeeding mode of development, the larvae of *P. vivipara* and *P. parvivipara* are minute, about 270 μm and 210 μm in length, respectively. Newly metamorphosed juveniles are about 240 μm and 310 μm in diameter, respectively. Post-metamorphic development involves substantial growth of the juveniles, which leave the parent at a diameter between 1.0 and 5.0 mm. The presence of a vestigial brachiolar complex and lecithotrophic development indicates that these species had a free-living lecithotrophic brachiolaria in their ancestry. We suggest that the evolution of viviparity in *Patiriella* sp. involved retention of a large egg by an ancestor that had a lecithotrophic brachiolaria followed by a secondary reduction in the size of the

ovum and simplification of the larva. The range of life histories seen in *Patiriella* is atypical of asteroid genera and supports the contention that the evolution of viviparity and other modes of modified development in the Asteroidea follows phylogenetic lineages.

Introduction

Asteroid echinoderms have diverse larval forms that are broadly divided into planktotrophic feeding larvae and nonfeeding lecithotrophic larvae. Possession of a small egg and a planktotrophic larva is generally accepted to be the ancestral mode of development in the Asteroidea, with evolution of nonfeeding development associated with acquisition of a large egg (Strathmann, 1978, 1993). An exception to this dichotomy is the viviparous development of the asterinid sea stars *Patiriella vivipara* and *P. parvivipara* (Byrne, 1991, 1996; Chia and Walker, 1991; O'Loughlin, 1991). These species have small eggs (135–150 μm diameter) similar in size to the eggs of a *Patiriella* species (*P. regularis*) that has planktotrophic development and considerably smaller than the eggs of *Patiriella* species that have lecithotrophic development (Table 1; Byrne and Barker, 1991). With the intragonadal location of the embryos, however, development of *P. vivipara* and *P. parvivipara* is clearly not planktotrophic. Despite the small size of their eggs, *P. vivipara* and *P. parvivipara* give birth to large (1.0–5.0 mm diameter) juveniles that are up to 30% of the diameter of the parent (Byrne, 1991, 1996). This substantial post-metamorphic growth is supported by intragonadal cannibalism.

Viviparity in *P. vivipara* and *P. parvivipara* is associated with the suite of life history traits often associated

Table 1

Size of eggs, larvae and newly metamorphosed juveniles of *Patiriella* species (SE, n)

Species	Oocyte: diameter (μm)	Brachiolaria larva: length (μm)	Newly metamorphosed juvenile: diameter (μm)
<i>Patiriella regularis</i>	150 (0.8, 20)	1430 (3.9, 20)	408.4 (9.0, 20)
<i>Patiriella calcar</i>	415 (3.7, 60)	746.9 (17.5, 10)	516.8 (18.3, 10)
<i>Patiriella gunni</i>	400 (1.9, 60)	490 (23.4, 12)	NA
<i>Patiriella exigua</i>	390 (4.3, 60)	690 (14.6, 7)	580 (18.9, 20)
<i>Patiriella vivipara</i>	148 (0.7, 21)	270 (8.1, 17)	314 (21.5, 12)
<i>Patiriella parvivipara</i>	135* (0.2)	207 (11.9, 12)	244 (9.3, 37)

NA, data not available.

* Largest primary oocytes seen in gonad.

with brooding in echinoderms (Byrne, 1991, 1996). Both of these species are small and hermaphroditic. *P. vivipara* has a maximum arm radius (R) of 15.0 mm, and *P. parvivipara*, the smallest known sea star, has a maximum radius of 5.0 mm (Dartnall, 1969; Keough and Dartnall, 1978; Byrne, 1996). Fertilization occurs in the gonads, most of which are ovotestes. The simultaneous presence of mature eggs and sperm in the gonads of *P. vivipara* and *P. parvivipara* creates the potential for self-fertilization.

Associated with their low-dispersal life history, *Patiriella vivipara* and *P. parvivipara* have the most restricted distribution known for the Asteroidea. *P. vivipara* is endemic to southeast Tasmania where it is recorded from four locations (Dartnall, 1969). *P. parvivipara* is restricted to the west side of the Eyre Peninsula in South Australia where it is recorded from five locations (Keough and Dartnall, 1978). Both species

have a geographic distribution of 150–300 km. These species are intertidal and inhabit about 100 m of the shoreline at each location where they occur. *P. vivipara* and *P. parvivipara* are morphologically similar to the sympatric species *P. exigua* and, prior to the observation of parturition, were considered to be variants of that species (Dartnall 1969, 1971; Keough and Dartnall, 1978). Systematists consider *P. vivipara* and *P. parvivipara* to be sibling species (Dartnall, 1971; Keough and Dartnall, 1978).

P. vivipara and *P. parvivipara* form part of a sympatric series of *Patiriella* species distributed around the Australian coast from Western Australia to north Queensland (Dartnall, 1971). The range of developmental patterns exhibited by *Patiriella* spans the broadcast-brooding continuum seen in the Asteroidea and is documented in a series of studies (Lawson-Kerr and Anderson, 1978; Byrne, 1991, 1992, 1995, 1996; Byrne and Barker, 1991; Chen and Chen, 1992; Byrne and Anderson, 1994; Cerra and Byrne, 1995a, b). Comparative life history data are available for eight species. *P. regularis* has the ancestral pattern of development through typical planktotrophic bipinnaria and brachiolaria larvae (Byrne and Barker, 1991). *P. gunni*, *P. calcar*, *P. brevispina*, and *P. pseudoexigua* develop through lecithotrophic planktonic brachiolariae, and *P. exigua* develops through a modified lecithotrophic benthic brachiolaria (Lawson-Kerr and Anderson, 1978; Byrne, 1991, 1992, 1995; Chen and Chen, 1992; Byrne and Anderson, 1994; Cerra and Byrne, 1995a, b). Documentation of the intragonadal development of *P. vivipara* and *P. parvivipara* in this study provides comparative data at the most derived end of this life-history series. With these contrasting modes of development, *Patiriella* presents an ideal model with which to

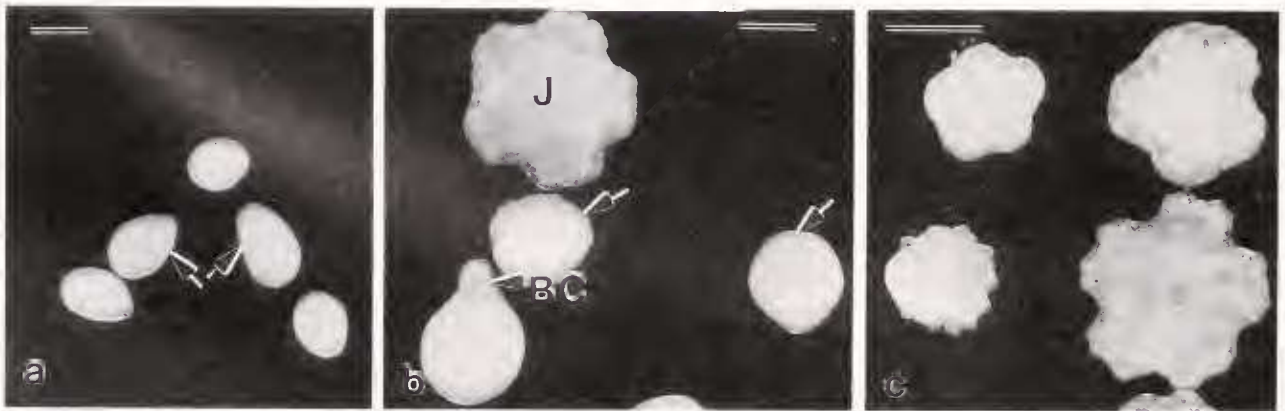


Figure 1. Light microscopy of development of live specimens of *Patiriella vivipara*. Scale bars = 160 μm . (a) Pear-shaped late gastrulae/early brachiolaria (arrows) freed from the gonad. (b) Metamorphosing larva (bottom left) with the brachiolar complex (BC) at the anterior end. Metamorphosis in the other larvae (arrows) is nearly complete. J, juvenile. (c) Metamorphosing (left) and recently metamorphosed juveniles (right).

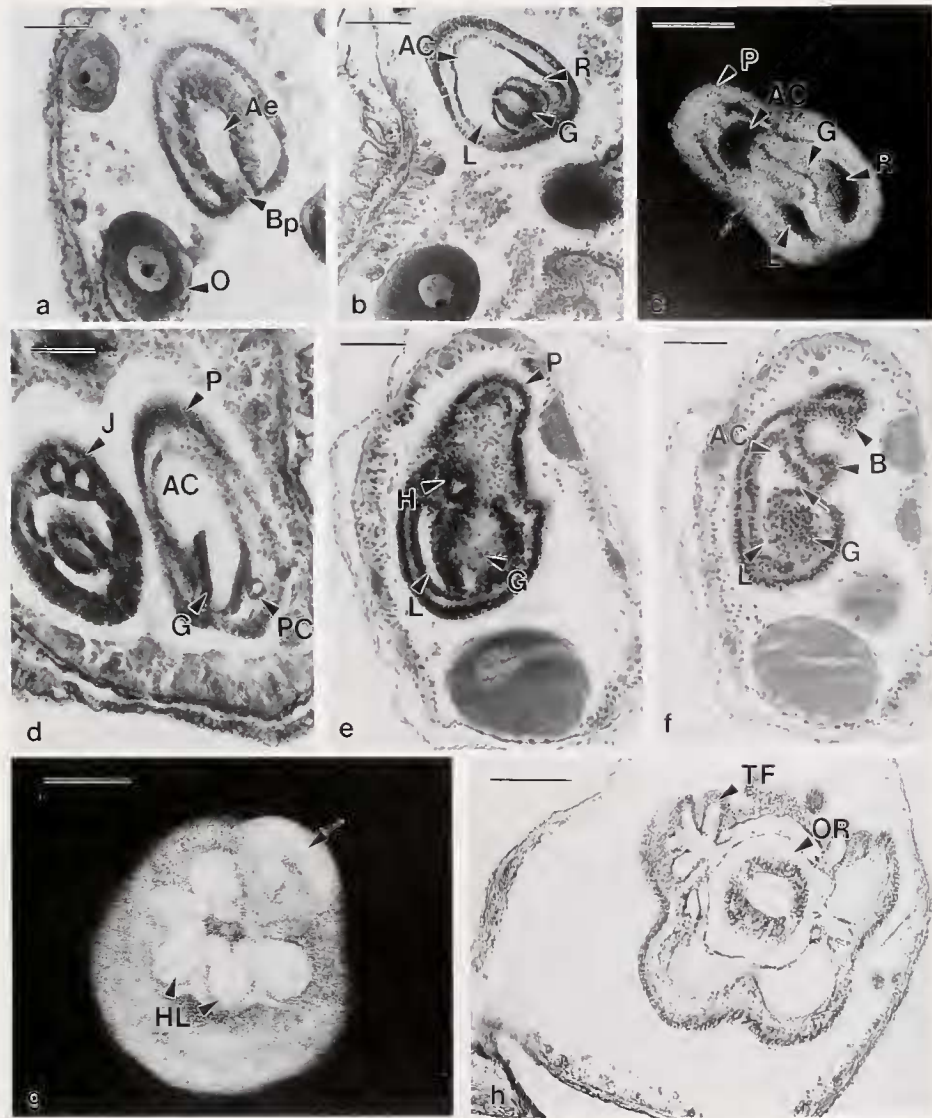


Figure 2. Light microscopy (Fig. 2a, b, d-f, h) and confocal microscopy (Fig. 2c, g) of internal development of *P. vivipara* (Fig. 2c, g) and *P. parvivipara* (Fig. 2a, b, d-f, h). Except in Fig. 2d, the larvae are orientated to facilitate presentation of right and left structures. Scale bars: Fig. 2a, b, d-f, h = 100 μ m; Fig. 2c, g = 50 μ m. (a) Gastrula with large archenteron (Ae) Bp, blastopore, O, oocyte. (b) Early brachiolaria with the large anterior coelom (AC) and left (L) and right (R) coeloms. G, gut. The left (L) and right (R) posterior coeloms have separated from the anterior coelom (AC). The arrow indicates the position of the hydrocoel, the five lobes of which were seen in the adjacent optical section. G, gut, P, preoral lobe. (d) Section of a brachiolaria showing the small posterior enterocoel (PC). AC, anterior coelom; G, gut; J, metamorphosing juvenile; P, preoral lobe. (e) Tangential section of a brachiolaria showing the hydrocoel (H), left posterior coelom (L) and gut (G). P, preoral lobe. (f) Grazing section through the brachiolaria in Figure 2e showing the extension (arrow) of the anterior coelom (AC) into the left brachium. B, brachia; G, gut; L, left coelom. (g) Metamorphosing brachiolaria with the resorbing larval body (arrow) between hydrocoel lobes (HL) one and five. (h) Newly metamorphosed juvenile with two pairs of tube feet (TF). OR, oral water ring.

address numerous hypotheses on life history evolution (Byrne, 1995). Most importantly, molecular data confirm that *Patiriella* is a monophyletic taxon (Hart, Byrne, and Smith, unpub.) and so the comparisons made here and elsewhere (Byrne, 1991, 1992, 1995; Byrne and

Anderson, 1994; Cerra and Byrne, 1995a, b) are not confounded by divergent phylogeny.

In this investigation, the intragonadal development of *P. vivipara* and *P. parvivipara* is documented in detail. The larvae of these species are compared with those

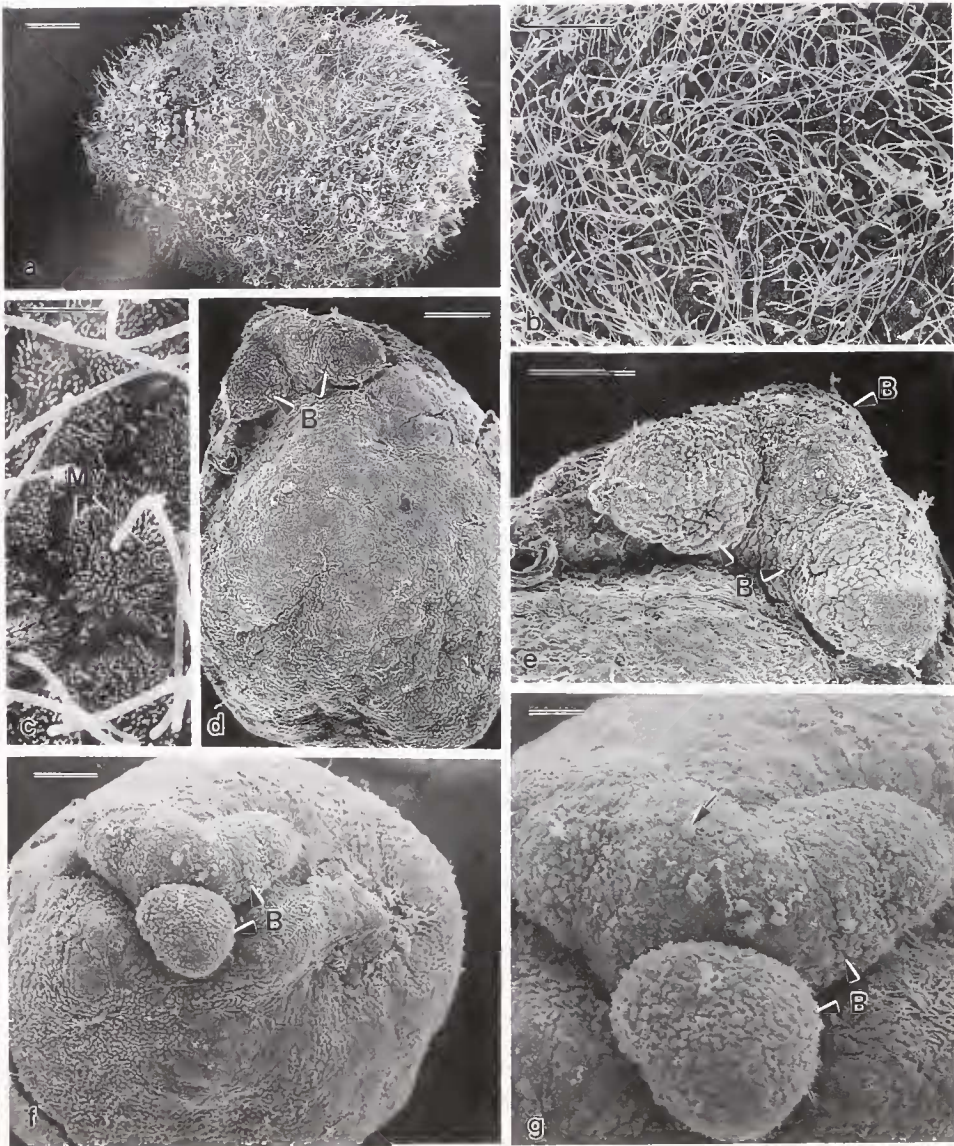


Figure 3. Scanning electron microscopy of pre-metamorphic development of *Patiriella vivipara* (Fig. 3b–g) and *P. parvivipara* (Fig. 3a). Scale bars: Fig. 3a, e = 20 μm ; Fig. 3b, g = 10 μm ; Fig. 3c = 2 μm ; Fig. 3d, f = 30 μm (a) Slightly elongate gastrula covered by cilia. (b) The cilia are evenly distributed across the epithelial surface. (c) Detail of the epithelial cells showing cilia (C) surrounded by microvilli (Mv). (d) Side view of a late brachiolaria. B, brachia. (e) Detail of the brachiolar complex. The third brachium (B) is just visible (top) on the other side of the larva. (f) Anterior view of a late brachiolaria. B, brachia. (g) Detail of the brachiolar complex showing the three brachia (B). The area where an attachment disc would be expected (arrow) is unspecialized.

of the other *Patiriella* species to assess the changes in larval form associated with the evolution of viviparity (Byrne, 1991; Byrne and Barker, 1991; Byrne and Anderson, 1994). Particular attention was paid to the presence of vestigial features in the larvae and, considering the small size of the eggs, it was of interest to determine whether development is of the feeding or nonfeeding type.

Materials and Methods

Specimens of *Patiriella vivipara* were collected in Tasmania from Midway Point (42°48' S; 147°32' E) and the Tessellated Pavement (43°31' S; 147°56' E). *P. parvivipara* was collected from Cape Vivonne (34°44' S; 135°52' E), South Australia. The developmental stages of these species were isolated by dissection of the gonads.

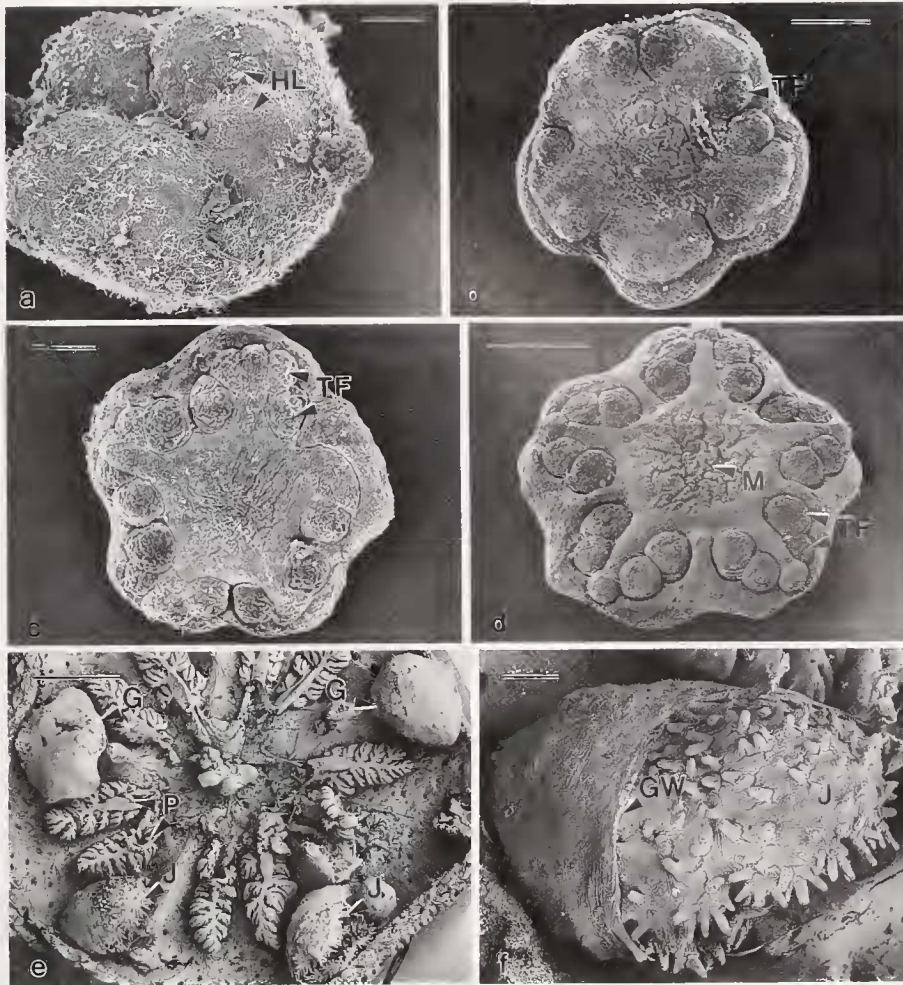


Figure 4. Scanning electron microscopy of metamorphosing juveniles and post-metamorphic development of *Patiriella vivipara* (Fig. 4a) and *P. parvivipara* (Fig. 4b–f). Scale bars: Fig. 4a = 30 μm ; Fig. 4b, c = 40 μm ; Fig. 4d = 100 μm ; Fig. 4e = 20 μm ; Fig. 4f = 300 μm (a) Metamorphosing juvenile with the larval body fully resorbed and the hydrocoel lobes (HL) developing on the oral side. (b) Juvenile with first pairs of tube feet (TF) forming. (c) Juvenile with second pair of tube feet (TF) forming. (d) Metamorphosed juvenile with developing mouth (M) opening. TF, tube feet. (e) Dissected adult showing advanced juveniles (J) developing in the gonads (G), P, pyloric caeca. (f) As the juveniles grow the gonad wall (GW) stretches to accommodate them.

The size of the oocytes and the intragonadal young were measured with an ocular micrometer. The larvae were measured along their length and the juveniles were measured across their maximum radius (R), from the center of the disc to the tip of one arm.

Development of *Patiriella vivipara* and *P. parvivipara* was documented by light microscopy (LM), confocal microscopy, and scanning electron microscopy (SEM). Live specimens were photographed with a photomicroscope. For histology, gonads or whole sea stars were fixed in Bouin's fluid or 2.5% glutaraldehyde in seawater. Following fixation, the tissues were dehydrated in graded ethanols, embedded in paraffin, and sectioned (6 μm

thick). Sections were stained with hematoxylin and eosin. For SEM, dissected embryos were fixed in 2.5% glutaraldehyde in filtered seawater for 1 h at room temperature. Following primary fixation, the specimens were washed in 2.5% NaHCO_3 (pH 7.2) and post-fixed in 2% OsO_4 in 1.25% NaHCO_3 for 1 h at room temperature. The specimens were then washed in distilled water and dehydrated in a graded series of ethanols, critical-point dried, sputter coated, and viewed with a JEOL JSM-35C scanning electron microscope.

For confocal microscopy, the larvae were fixed in 2% paraformaldehyde in seawater. The larvae were then dehydrated in graded ethanols, cleared in Histo-Clear (Na-

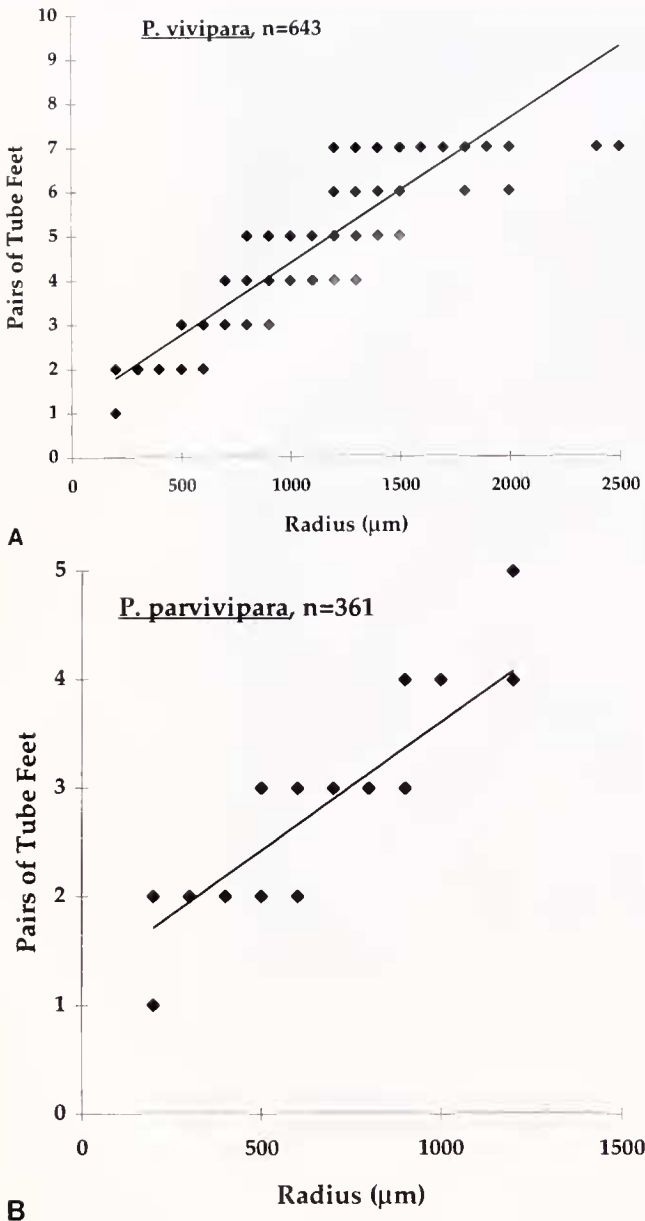


Figure 5. The relationship between the size of the intragonadal juveniles and the number of tube feet. (A) *Patiriella vivipara*, $r^2 = 0.845$. (B) *P. parvivipara* $r^2 = 0.710$. R = radius.

tional Diagnostics; Atlanta, Georgia), and mounted on slides. Optical sections of the specimens were made with a BIO-RAD MRC600 confocal microscope.

Development of the skeleton was documented by utilizing the birefringent properties of the calcite ossicles. The larvae are opaque and whole mounts of early larvae fixed in glutaraldehyde, dehydrated in alcohol, and cleared in Histo-Clear were observed with polarized light.

The sizes of the brachiolaria and newly metamorphosed juveniles of *P. vivipara* and *P. parvivipara* were

compared with these developmental stages in other *Patiriella* species. For *P. regularis*, *P. exigua*, and *P. calcar*, live larvae were measured with an ocular micrometer. For *P. gumii*, measurements were made from photographs of live larvae. Measurements of newly metamorphosed *P. exigua* were made from live specimens. Measurements of newly metamorphosed *P. calcar* and *P. regularis* were made from preserved specimens.

Results

Pre-metamorphic development

Patiriella vivipara and *P. parvivipara* have the same pattern of development. Except where noted, the following description applies to both species.

The largest eggs encountered in the ovotestes of *P. vivipara* were pale orange primary oocytes and ova. These eggs had a mean diameter of $148 \mu\text{m}$ ($\text{SE} = 0.7$, $n = 21$). Ova were not encountered in the gonads of *P. parvivipara*. For this species, the largest eggs seen were $135 \mu\text{m}$ diameter ($n = 2$).

When the gonad was torn during dissection, minute gastrulae and brachiolaria larvae were released and swam in the seawater in the dissection dish (Fig. 1a, b). Due to the intragonadal location of the embryos, they were often surrounded by gametes (Fig. 2a, b, e, f). Development proceeded through the wrinkled blastula and gastrula stages. The gastrulae were uniformly ciliated and swam, propelled by the cilia, in the gonadal fluid (Figs. 2a, 3a–c). Each epithelial cell had one cilium surrounded by a field of microvilli (Fig. 3c). At no stage in development were the embryos attached to the gonadal wall. The gastrulae were round to elongate (Figs. 2a, 3a). This stage in *P. vivipara* had a mean length of $183 \mu\text{m}$ ($\text{SE} = 3.8$, $n = 5$) and in *P. parvivipara* had a mean length of $140 \mu\text{m}$ ($\text{SE} = 0$, $n = 5$). The blastopore closed as the gastrulae elongated.

The gastrulae gave rise to pear-shaped brachiolaria larvae that had a reduced brachiolar complex (Figs. 1a, b, 2c–f, 3d–g). Most of the larvae encountered had the simple pear-shaped profile seen in Fig. 2c. The larvae rotated as they swam with their anterior end forward. In *P. vivipara* these larvae had a mean length of $270 \mu\text{m}$ ($\text{SE} = 8.0$, $n = 17$), and in *P. parvivipara* they had a mean length of $207 \mu\text{m}$ ($\text{SE} = 1.9$, $n = 12$). The anterior preoral lobe of these larvae corresponds to the central brachiolar arm or brachium of planktonic brachiolaria. Two lateral extensions of the body developed at the base of the preoral lobe to form the right and left brachia, thereby completing the brachiolar complex. The area at the base of the arms, where an attachment disc would be expected to form, remained unspecialized (Fig. 3f, g). In *P. vivipara* and *P. parvivipara*, the brachiolar complex does not function as a larval attachment organ.

Internal development involved formation of one large enterocoel at the anterior end of the archenteron and one small posterior enterocoel on the left side of the archenteron (Fig. 2b–d). The anterior coelom extended into the preoral lobe and gave rise to the left and right coeloms on either side of the body (Fig. 2b, c, e, f). This coelom also gave rise to two short coeloms that extended into the lateral brachia (Fig. 2f). The hydrocoel developed on the left side of the larva soon after the brachiolaria stage was reached (Fig. 2c, e).

The brachiolaria metamorphosed in the gonadal lumen with formation of the juvenile at the rounded posterior end and reduction of the preoral lobe (Figs. 1b, 2g). On scanning view, the preoral lobe was composed of three small brachia (Fig. 3d–g). The ciliary cover was reduced (Fig. 3d, f). Metamorphosing larvae tended to spin around in one place. As the hydrocoel developed, the larval body was resorbed between hydrocoel lobes 1 and 5 (Fig. 2g). The rudiments of the adult skeleton appeared as birefringent spicules in metamorphosing larvae at a length of about 200 μm .

The rudiments of the adult arms and developing tube feet were evident on the oral side of metamorphosing juveniles (Figs. 1c, 2h, 4a–d). Metamorphosing larvae and newly metamorphosed juveniles had a mean diameter of 314 μm (SE = 21.5, $n = 12$) in *P. vivipara* and 244 μm (SE = 9.3, $n = 37$) in *P. parvivipara*. These larvae and newly metamorphosed stars were pale yellow. The mouth opened after the second pair of tube feet developed at about 400 μm diameter (Figs. 2h, 4d).

Post-metamorphic growth

Post-metamorphic development involved an increase in size of the juvenile and the addition of pairs of tube feet. The relationship between the number of tube feet and size of the juveniles is shown in Figure 5A, B. The largest intragonadal juvenile of *P. vivipara* had a radius of 2.5 mm and had 8 pairs of tube feet. In *P. parvivipara*, the largest intragonadal juvenile had a radius of 1.2 mm and 5 pairs of tube feet. The gonad wall stretched to accommodate growth of the juveniles (Fig. 4e, f).

Discussion

The presence of vestigial structures provides important evidence for elucidating the direction of evolutionary change (Strathmann, 1993). In *Patiriella vivipara* and *P. parvivipara*, the brachiolar complex is a vestigial remnant of the complex present in the other *Patiriella* species that use it for benthic attachment during metamorphosis. Metamorphosis in the *P. vivipara* and *P. parvivipara* does not involve attachment, and so the brachiolar complex is correspondingly reduced and nonfunctional. Not surprisingly, there is no trace of a plank-

trophic bipinnaria larva with the larval gut forming a closed structure that serves as a rudiment for the adult gut. The possession of a vestigial brachiolar complex and lecithotrophic development indicates that *P. vivipara* and *P. parvivipara* had a free-living lecithotrophic brachiolaria in their ancestry. The highly modified ontogenies of these species support the contention that viviparity is a derived life history positioned at the extreme end of the broadcasting–brooding continuum of life histories seen in *Patiriella* (Fig. 6).

With their central brachium and two lateral brachia, the larvae of *P. vivipara* and *P. parvivipara* are particularly similar to the early brachiolaria of the other *Patiriella* with lecithotrophic development (Byrne, 1995). In contrast to the viviparous species, however, brachiolar growth in the planktonic lecithotrophs involves further development of the arms, with the central brachium forming a conspicuous ventral curvature (Fig. 6; Byrne, 1991; Byrne and Anderson, 1994). Brachiolar growth in the benthic lecithotroph *P. exigua* results in formation of a tripod-shaped larva due to hypertrophic growth of the lateral brachia (Fig. 6; Byrne, 1995).

Pre-metamorphic development in *P. vivipara* and *P. parvivipara* appears to be largely supported by the vitellogenic reserves present in the egg. Although these reserves may be augmented by nutrients present in the gonadal fluid, the small size of the larvae indicates that dependence on extraembryonic nutrition is minimal. Unlike other asteroids with lecithotrophic development, including several *Patiriella* species, *P. vivipara* and *P. parvivipara* have a minute egg (Table 1, Fig. 6). As a result, the larvae and newly metamorphosed juveniles of these viviparous species are considerably smaller than those of their lecithotrophic congeners (Table 1). In contrast, the recruiting juveniles are the largest reported for the Asteroidea. Rather than channeling vitellogenic reserves into making large eggs, *P. vivipara* and *P. parvivipara* use cannibalism to support development at the post-metamorphic stage (Byrne, 1996). Parental investment by *P. vivipara* and *P. parvivipara* clearly favors the post-metamorphic progeny that may be incubated in the gonads for up to one year (Byrne, 1996).

Viviparity is rare in the Asteroidea. The only other asteroid known to have intragonadal development is another asterinid species, *Asterina pseudoexigua pacifica* (Table II, Komatsu *et al.*, 1990). Like *Patiriella vivipara* and *P. parvivipara*, the larvae of *A. pseudoexigua pacifica* are lecithotrophic (Komatsu *et al.*, 1990). In contrast to the minute brachiolaria of *P. vivipara* and *P. parvivipara*, the intragonadal brachiolaria of *A. pseudoexigua pacifica* is similar in size and form to planktonic lecithotrophic brachiolaria, and its development is supported by nutrients present in a large egg (450 μm diameter) (Komatsu *et al.*, 1990).

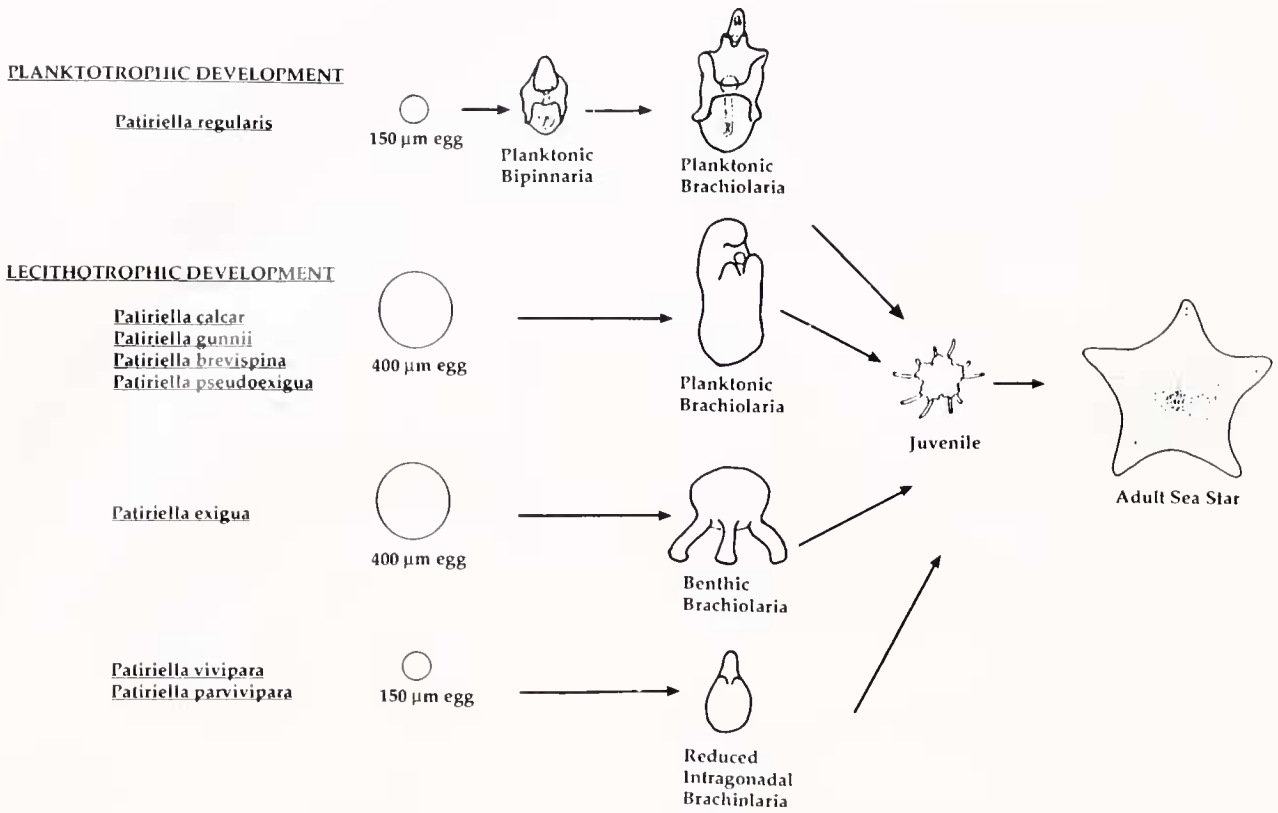


Figure 6. Diagram illustrating the developmental patterns of *Patiriella* species with the development of *P. regularis* (top) presumed to represent the ancestral state. Viviparity in *P. vivipara* and *P. parvivipara* is suggested to have arisen *via* an intermediate ancestor with benthic lecithotrophy. The evolutionary changes in developmental pattern are suggested to be from planktotrophy to planktonic lecithotrophy to benthic lecithotrophy to viviparity.

P. vivipara and *P. parvivipara* are unique among lecithotrophic asteroids in having a small egg. This prompts the question as to whether the evolution of viviparity in these species involved the retention of a small egg in the gonads for fertilization or retention of a large egg with a secondary reduction in egg size. Insights into this question are provided by systematic evidence and mtDNA sequence data (Dartnall, 1969, 1971; Keough and Dartnall, 1978; Hart, Byrne, and Smith, unpub.). On the basis of adult morphology, systematists place *P. vivipara* and *P. parvivipara* in the 'exigua' group and suggest that they were derived from an *exigua*-like ancestor (Dartnall, 1971; Keough and Dartnall, 1978). Distinguishing the species in this group depends on life-history characters and in archived collections often requires examination of the gonads for brooded young (Keough and Dartnall, 1978). Molecular data support inclusion of *P. vivipara* and *P. parvivipara* in the 'exigua' group and indicate that the viviparous *Patiriella* species diverged from an *exigua*-like ancestor approximately 3 million years ago (Hart, Byrne, and Smith, unpub.).

P. exigua deposits large eggs onto the substratum and abandons the developing embryos (Byrne, 1995). It has been suggested that the benthic life history of *P. exigua* may have set the stage for the evolution of intragonadal brooding in *Patiriella* (Byrne, 1991, 1995). Deposition of egg masses would have made the evolution of external brooding a relatively simple matter of the adult remaining with the egg mass, as exemplified by several closely related *Asterina* species (Table II, Strathmann *et al.*, 1984). In the proposed sequence of events it is suggested that intragonadal brooding arose from retention of eggs by an external brooder as occasionally occurs in *A. phylactica* (Strathmann *et al.*, 1984). We suggest that the transition to viviparity in *Patiriella* was from benthic lecithotrophy to intragonadal brooding as outlined in Figure 6. This transition would have involved retention of a large ovum for internal fertilization followed by a secondary reduction in egg size. This secondary reduction would have occurred in parallel with the evolution of intragonadal cannibalism to ensure that the juveniles emerge at a large size. The intragonadal location of the

Table II

Developmental patterns and larval types in the Family Asterinidae

Genus	Species	Spawning/Fertilization	Developmental pattern	Larval type (s)
<i>Patiriella</i>	<i>P. regularis</i>	Broadcaster	Planktotrophy	Bipinnaria and brachiolaria
	<i>P. calcar</i>	Broadcaster	Planktonic lecithotrophy	Brachiolaria
	<i>P. gunnii</i>	Broadcaster	Planktonic lecithotrophy	Brachiolaria
	<i>P. brevispina</i>	Broadcaster	Planktonic lecithotrophy	Brachiolaria
	<i>P. pseudoexigua</i>	Broadcaster	Planktonic lecithotrophy	Brachiolaria
	<i>P. exigua</i>	Deposits egg masses	Benthic lecithotrophy	Tripod brachiolaria
	<i>P. vivipara</i>	Intragonadal fertilization	Viviparous lecithotrophy	Reduced brachiolaria
	<i>P. parvivipara</i>	Intragonadal fertilization	Viviparous lecithotrophy	Reduced brachiolaria
<i>Asterina</i>	<i>A. pectinifera</i>	Broadcaster	Planktotrophy	Bipinnaria and brachiolaria
	<i>A. miniata</i>	Broadcaster	Planktotrophy	Bipinnaria and brachiolaria
	<i>A. batheri</i>	Broadcaster	Planktonic lecithotrophy	Brachiolaria
	<i>A. burtoni</i>	Broadcaster	Planktonic lecithotrophy	Brachiolaria
	<i>A. coronata japonica</i>	Broadcaster	Planktonic lecithotrophy	Brachiolaria
	<i>A. minor</i>	Deposits egg masses	Benthic lecithotrophy	Tripod brachiolaria
	<i>A. gibbosa</i>	Deposits egg masses	Benthic lecithotrophy	Brachiolaria with a foot-like attachment complex
	<i>A. phylactica</i>	Broods egg masses	Benthic lecithotrophy	Brachiolaria with a foot-like attachment complex
	<i>A. atyphoida</i>	Broods egg masses	Benthic lecithotrophy	—
	<i>A. scobinata</i>	Broods egg masses	Benthic lecithotrophy	—
	<i>A. pseudoexigua pacifica</i>	Intragonadal fertilization	Viviparous lecithotrophy	Brachiolaria

Data from MacBride, 1896; Dartnall, 1970; James, 1972; Komatsu, 1975; Kano and Komatsu, 1978; Komatsu *et al.*, 1979; Marthy, 1980; Strathmann, 1987; Byrne, 1991, 1992, 1995, 1996; Chen and Chen, 1992; Chia *et al.*, 1993.

larvae would have released them from selective pressures to maintain the brachiolar complex, resulting in the simplification of the larval form.

The influence that developmental evolution has exerted on speciation in *Patiriella* is exemplified by *P. vivipara* and *P. parvivipara*. The morphological overlap between the phenotype and ecologies of adult *P. vivipara*, *P. parvivipara*, and *P. exigua* contrasts with the different phenotypes and ecologies of their larvae (Fig. 6). This contrast indicates that selection on the developmental stages has played an important role in the divergence of these three species. It also supports the suggestion of a decoupling of selective pressures on the adult and larval stages of *Patiriella* such that adult and larval stages respond differently to selective pressures during their evolution (Byrne and Anderson, 1994). This phenomenon is undoubtedly of great importance in taxa such as echinoderms which have complex life histories (Raff, 1992; Byrne and Anderson, 1994; Wray, 1995). With the divergence time between the viviparous species and *P. exigua* estimated to be 3 million years, it appears that evolution of viviparity was relatively rapid (Hart, Byrne, and Smith, unpub.). Rapid evolution of development is also reported for the sea urchin genus *Heliocidar* (Smith *et al.*, 1990; Wray, 1995).

The extremely limited distributions of *P. vivipara* and *P. parvivipara*, together with their extended brood care,

indicate that their ranges are unlikely to increase and that they may be heading towards extinction. The distribution of *P. vivipara*, with two of the populations on either side of a 60-km-long peninsula, suggests that the present distribution of this species is a remnant of a previously wider range. Considering the important insights on life-history evolution that can be obtained through investigation of these unusual species, it is fortunate that they are extant. This scientific importance highlights *P. vivipara* and *P. parvivipara* as candidates for conservation.

Although it is not known whether brooding has imparted a selective advantage (or disadvantage) for *P. vivipara* and *P. parvivipara*, comparative embryology and systematic evidence suggest that evolution of viviparity was central to their divergence. The systematic distribution of brooding and other patterns of modified development appears to be skewed to certain echinoderm clades (Emler, 1990; Pearse and Bosch, 1994). In the Asteroidea, the Family Asterinidae is a particularly illustrative example (Table II). In addition to *Patiriella*, the genus *Asterina* contains species with life histories that cover the broadcast-brooding continuum of life histories seen in the Asteroidea (Table II). Like *Patiriella*, *Asterina* species have developmental patterns ranging from planktotrophy to viviparity (Table II). There are also several fissiparous *Asterina* species (Achituv, 1969; Marsh, 1977). The developmental diversity seen in *Patiriella* and *Ast-*

erina is atypical of asteroid genera and supports the contention that the evolution of modified patterns of development in the Asteroidea and other echinoderms follows phylogenetic lineages (Pearse and Bosch, 1994).

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